THE ROLE OF SOIL ANIMALS IN BREAKDOWN OF LEAF MATERIAL

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Introduction

Much remains to be discovered about the relative importance of soil animals, fungi and bacteria in the breakdown of leaf material that falls on to the surface of the soil, or is incorporated into it. NEF (1957), who reviewed the subject, thought that soil animals not only fragment and mix leaf litter with soil, but also cause chemical changes that enable bacteria and fungi to decompose it further. KURCHEVA (1960) found that oak-leaf litter lost half its weight in 140 days when animals were not excluded, but only one-tenth of its weight when they were excluded with naphthalene. He concluded that bacteria and fungi alone break down litter only very slowly. VAN DER DRIFT (1958) thought the soil fauna important mainly in the mechanical destruction of leaves, so making them a suitable substrate for smaller animals and micro-organisms. All these workers measured breakdown by change in weight of litter.

In our work leaves were exposed to various fractions of the soil fauna and rate of breakdown was assessed by measuring the area of leaf lamina eaten.

Material and Methods

The initial experiment was in an oak dominant mixed woodland (Geescroft, Rothamsted) with soil that can be described as an earthworm mull. Two hundred $2\frac{1}{2}$ cm diameter discs, cut from the centre of freshly fallen oak leaves, were laid out evenly on one square metre of bare soil and covered with a 0.7 mm mesh terylene net supported by a wooden frame; on top of the mesh a layer of normal leaf litter was placed. The soil arthropods present were studied in detail (MADGE, 1961) and the numbers of earthworms were estimated by a formalin sampling method (RAW, 1959). The leaf discs were examined at weekly intervals, by lifting the frame and

superficial litter. The onset of fragmentation and eventual disappearance of discs was recorded, but the exact amount of material that had disappeared from each disc was not determined.

In the second experiment leaves were collected from oak and beech trees during July and 2½ cm diameter discs cut from them. Nylon mesh bags, 10 cm × 7 cm, were made from the following meshes, which only allowed certain organisms to enter:

1. 7 mm openings .... all micro-organisms and invertebrates.
2. 1 mm openings .... all micro-organisms and invertebrates, except earthworms.
3. 0.5 mm openings .... only micro-organisms, mites, springtails, enchytraeids and small invertebrates.
4. 0.003 mm openings .... only micro-organisms.

Fifty leaf discs were placed in each bag and buried 2½ cm deep in newly-cultivated, old pasture soil (Highfield, Rothamsted) with one bag of each mesh size in each of four separate plots, measuring 2.75 metres square. Every two months the bags were dug up, the discs removed from each bag in turn and placed between two sheets of glass held together by spring clips. At the same time the animals found between the discs were counted. A grid with the area of a leaf disc divided into 100 squares, engraved on clear perspex, was used to estimate the percentage loss of tissue by holding it over each disc in turn with a light behind the glass. The estimates were made as rapidly as possible, the bags of discs being kept at 5° C until they could be dealt with, and then buried in a new position in the plot. The accuracy was checked by duplicate estimates and by comparison with the figure obtained with an apparatus that estimates a leaf area photo-electrically (ORCHARD, 1958).

Fig. 1. Leaf discs eaten by various invertebrates.

The plots used were the untreated controls of a larger experiment, which compared the effect of different levels of DDT and aldrin on the breakdown of discs buried in the plots.

The fauna of the plots were also studied in detail to get information on the seasonal changes in numbers of the different groups of animals.

Results

The graph in Fig. 2 summarizes the results of the initial experiment; numbers of the common groups of animals found on this site are listed below (Table 1). Earthworms fragmented and removed by far the largest proportion of the discs; after one year, none of the leaf discs remained intact and all but 8 % had disappeared. Several times between April and October when there was heavy rain discs disappeared more rapidly than in dry periods.

Fig. 3 shows results from the second experiment, only the disappearance from 7 mm and 0.5 mm mesh bags has been plotted, because results with

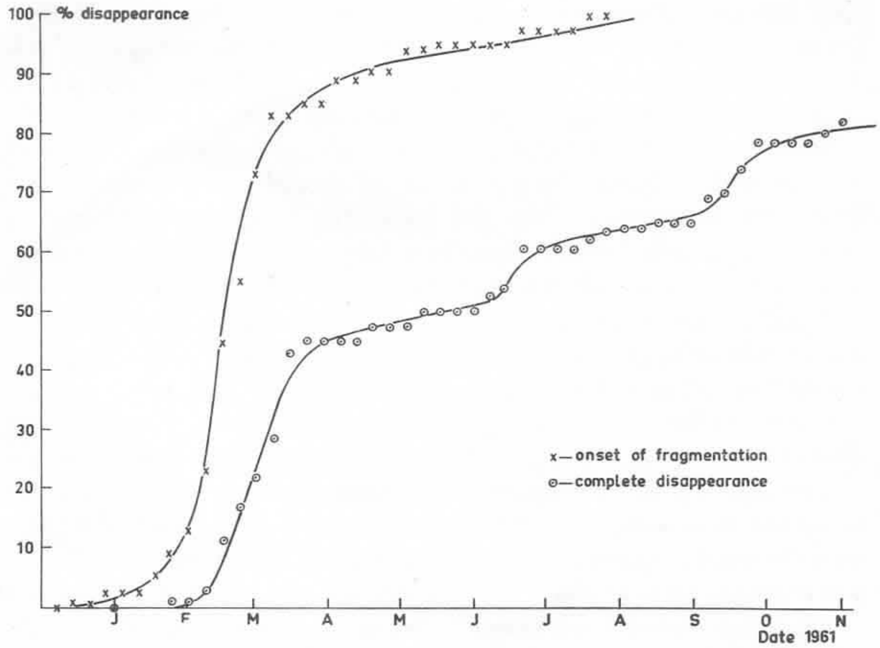

Fig. 2. Decomposition of leaf discs.

TABLE 1. Fauna of Geescroft, the site of the first experiment

	Average number per square metre		Av. weight
Earthworms*			
Lumbricus terrestris		18.0	12.6 g
L. rubellus		44.8	
L. castaneus			
Allolobophora longa			24.1 g
A. caliginosa		5.4	
Dendrobaena subrubicunda			
A. nocturna			
Total		68.2	36.7 g
Other Invertebrates**			
Acarina		7,250	
Oribatidae	6,250		
Collembola		1,350	
Other arthropods		500	
Total		9,100	

* Sampled in April.
** Means of monthly sampling.

the 1 mm and 0.5 mm bags were too similar to need including. Further, 1 mm mesh bags did not always exclude earthworms, and rates of disappearance consequently differed greatly between individual bags. In the bags with smaller than 0.003 mm mesh, the discs remained intact; although a few tiny springtails and enchytraeid worms penetrated these bags apparently they did not feed. During this experiment leaf discs gradually changed colour from green to greenish yellow and brown but there was relatively little variation in colour between discs. In a later experiment with apparently similar green leaves collected from beech trees in September, there was variation in colour changes. Some discs remained quite green and were quickly attacked; others became dark brown and were not appreciably attacked by soil animals even after nine months.

Where the leaves were packed closely together within the bags those discs in the centre were attacked by small arthropods first. Some distinction was possible between the feeding of earthworms, enchytraeids, dipterous larvae and small arthropods (Fig. 1). The last parts of the discs to disappear were the woody veins which sometimes persisted throughout the sampling period even in the large mesh bags. Whether discs were moist or dry appeared to affect their susceptibility to attack by soil animals, as in the first experiment. Table 2 lists the numbers of animals found on this site.

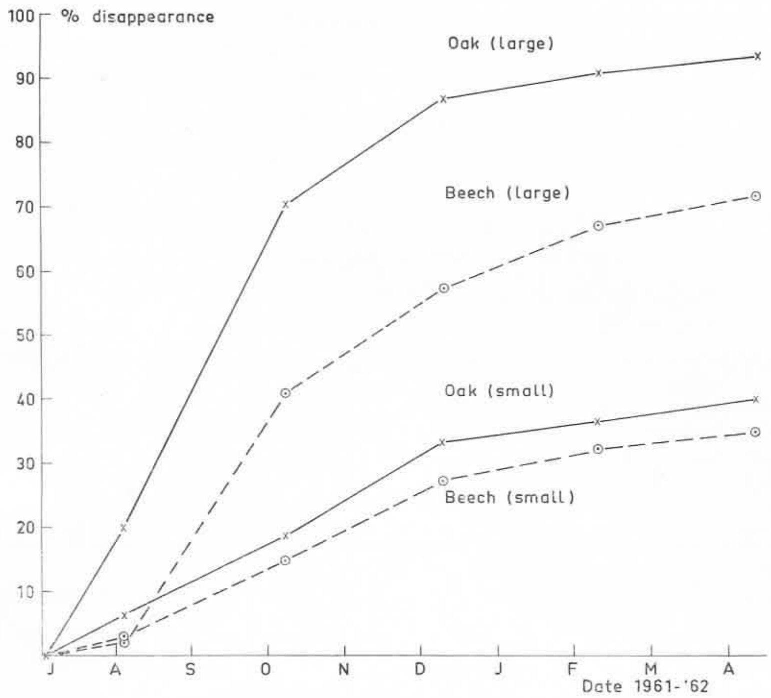

Fig. 3. Decomposition of leaf discs by soil animals.
Oak, large: Oak leaf discs in 7 mm mesh bags.
Beech, large: Beech leaf discs in 7 mm mesh bags.
Oak, small: Oak leaf discs in 0.5 mm mesh bags.
Beech, small: Beech leaf discs in 0.5 mm mesh bags.

Discussion

Previous investigators measured breakdown by changes in weight of samples of leaves or litter over different periods, which gave little idea of the relative importance of animals in leaf breakdown. The method used here, visual estimation of tissue eaten, separated breakdown by soil animals from that by micro-organisms. An important aspect of this work is the technique of exposing leaf tissue to different fractions of the soil fauna, and to micro-organisms alone, by using bags of different meshes: this gives data on the relative importance of different organisms in leaf breakdown. Results obtained with these techniques had to take account of the numbers of animals found inside the bags, because animals such as earthworms can

TABLE 2. Fauna of Highfield, the site of the second experiment

	Average number per square metre		Av. weight
Earthworms*			
Lumbricus terrestris		24.2	20.4 g
L. rubellus			
L. castaneus			
Allolobophora nocturna		40.5	18.7 g
A. caliginosa			
Total		64.7	39.1 g
Other Invertebrates**			
Acarina		24,600	
Oribatidae	16,600		
Collembola		18,500	
Onychiuridae	12,600		
Isotomidae	5,000		
Other arthropods		1,600	
Total		44,700	

* Sampled in April.
** Means of monthly sampling.

enter a bag when very small and after growing, become trapped inside; careful selection of mesh sizes can minimize this.

The first experiment indicated that earthworms were the most important animals in breaking down leaves, but there were few other invertebrates present on this site, whereas earthworms were unusually plentiful for a woodland soil. These facts were in keeping with the character of the soil, which was a good earthworm mull on a fertile brown earth. Fig. 2 shows that the curve for onset of fragmentation was much smoother than that for complete disappearance of the leaf discs. One explanation of this may be that whereas initial fragmentation of the discs was largely by the smaller arthropods, their final disappearance was caused by earthworms, which are more sensitive to moisture changes than the arthropods.

The second site had a more balanced fauna and the mesh bags enabled the role of the different sections of the fauna in breakdown to be determined more exactly. For instance, the leaf discs in the largest mesh bags disappeared about three times as quickly as those in the 0.5 mm mesh. Enchytraeid worms, often found inside these small-mesh bags, seemed unable to feed until there had been some fragmentation by Collembola and dipterous larvae, which appeared to be principally responsible for fragmentation.

Although there were very many Oribatid mites in the surrounding soil, there was no evidence that they contributed to the leaf breakdown. The only animals found inside the mesh bags were earthworms, enchytraeid-worms, springtails, dipterous larvae and predatory mites.

Further evidence of the role of small soil animals was provided by the breakdown of leaf discs in plots treated with insecticides. Aldrin greatly decreased the numbers of springtails and dipterous larvae, and there was a corresponding decrease in the rate leaf tissue disappeared in small mesh bags. By contrast DDT increased numbers of springtails and the rate of leaf fragmentation.

Both experiments showed that the condition of the leaf was important in determining its rate and type of breakdown. For example, when seemingly similar leaf discs were exposed to soil animals, some turned brown, became tanned and remained intact, whereas those that remained green or turned yellow were heavily attacked. HANDLEY (1961) gives a possible explanation for this in that the increase in polyphenolic materials in leaves between July and September precipitates protein complexes, making them less digestible, as well as masking cellulose. Thus plant material which reaches the soil before this has happened is probably more susceptible to breakdown by soil animals.

Rate of breakdown also depends on species of leaf; as can be seen in Fig. 3, oak disappeared considerably faster than beech. Beech leaves not only resisted attack by soil arthropods more but were much less palatable to earthworms, than oak leaves, although this was most noticeable during the first three months of breakdown. Dry discs broke down slowly; the rate increased when they became moist (Fig. 2). When the discs were buried and thus kept damp, as in the second experiment, they disappeared much faster than when laid on the soil surface. Since the numbers of earthworms were of the same order on both sites, this difference probably reflects the moisture content of the discs. The less woody parts of the discs were the first to disappear, even when attacked by earthworms.

The second experiment showed that the fungi and bacteria above contributed no visible effect to breakdown of leaves in the absence of soil animals. Leaf discs from which soil animals were excluded appeared to remain intact, but they could not be weighed without oven-drying them and so spoiling them for further use. A previous experiment showed that samples from litter of leaf lamina undamaged by animals showed no significant decrease in weight per unit area, over a period of twelve months. It remains

to be shown how far breakdown would proceed with soil animals present but without micro-organisms.

Summary

Breakdown of leaf tissue was investigated by visual estimation of disappearance of leaf discs. Discs were placed under litter or buried in bags of several meshes to exclude soil animals differentially. Earthworms removed discs three times faster than smaller invertebrates, most important of which were springtails, enchytraeids and dipterous larvae. Oak discs disappeared faster than beech. Some discs cut from beech leaves picked in September, became tanned and remained uneaten, whilst those which did not, were heavily attacked. When animals were completely excluded for nine months no visible breakdown occurred.

References

DRIFT, J. VAN DER, 1958. The role of the soil fauna in the decomposition of forest litter. Proceedings of the XVth International Congress of Zoology, London, 357—360.

HANDLEY, W. R. C., 1961. Further evidence for the importance of residual leaf protein complexes in litter decomposition. Plant and Soil, **15** , 37—74.

KURCHEVA, G. F., 1960. The role of invertebrates in the decomposition of oak litter. Pedology, Leningr., **4**, 16—23.

MADGE, D. S., 1961. Some aspects of the ecology and physiology of free living mites. Ph. D. Thesis. University of London.

NEF, L., 1957. État actuel des connaissances sur le rôle des animaux dans la décomposition des littières de forêts. Agricultura, Louvain, **5** (3), 245—316.

ORCHARD, B., 1958. Measurement of leaf area. Rep. Rothamst. exp. Sta., **81**.

RAW, F., 1959. Estimating earthworm populations by using formalin. Nature, Lond., **184**, 1661.

Discussion

A. BURGES: If area is used as a measure in decomposition of *Pinus* or *Casuarina* the result would be very false. Up to 60 % of dry weight may be lost with no noticeable change in area

G. W. HEATH: We have not used such material, only broad-leaved trees.

A. MACFADYEN: An area measurement will not reveal Oribatidae that have penetrated the leaves or those feeding on detached pieces of leaf and earthworm faeces. Could this account for the failure to find oribatid mites and to attribute any importance to them in these experiments?

G. W. HEATH: Not only have we been unable to find any effect by Oribatids in primary breakdown, but we have never actually found Oribatids on the discs. We are sure that they were not tunnelling inside the leaf lamina. These investigations are done on good earthworm mull soils, where the Oribatids are very few in number. It is possible that the mites are indeed important in subsequent breakdown and that many feed on earthworm excreta. We have not yet investigated such subsequent breakdown.

D. A. VAN SCHREVEN: It would be interesting to study the breakdown when only one

disc, instead of 50, is placed in each bag with the smallest openings as in your experiments. The microbial breakdown depends not only on the C/N ratio of the organic matter but also on the mineral nitrogen in the soil surrounding it. The effect of the latter factor is greatly decreased when there are many discs in each bag and would be much greater with only one disc in a bag.

G. W. HEATH: This may be so, but in the early work referred to in the paper, no loss of weight per unit area could be detected in the uneaten portions of beech or oak leaves allowed to lie freely on the litter surface. Such leaves are dry for most of the time and therefore microbial activity may not proceed very far. Such restrictions as you mention perhaps are operating amongst the packed leaves, but one would not expect this to be so where the discs on the outside of the clump are concerned. No difference between these discs and those inside the clump could be detected.

I. N. HEALEY: Do you know whether the onychiurid Collembola present in the bags were feeding directly on plant material or on fungal hyphae bacteria etc. Have you examined their guts?

C. A. EDWARDS: We did not examine the guts, but from other field experiments we have evidence that they may be primary feeders and will in fact feed even on living plantmaterial.